

Ailuropoda melanoleuca. By John Chorn and Robert S. Hoffmann

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Ailuropoda Milne-Edwards, 1870

Ailuropoda Milne-Edwards, 1870:1. Type species *Ursus melanoleucus* David, 1869, by monotypy.

Pandarctos Gervais, 1870:161. Renaming of *Ursus melanoleucus* David, 1869.

Ailuropus Milne-Edwards, 1871:88. Replacement for *Ailuropoda* Milne-Edwards, 1870, believed preoccupied.

Aeluropus Flower and Lydekker, 1891:560. Emendation of *Ailuropus* Milne-Edwards, 1871.

CONTEXT AND CONTENT. Order Carnivora, Superfamily Canoidea, Family Ursidae, Subfamily Agriotheriinae, Tribe Ailuropodini (Hendey, 1972; see also Winge, 1895-96, and Erdbrink, 1953). The genus *Ailuropoda* contains one living species, *Ailuropoda melanoleuca*.

***Ailuropoda melanoleuca* (David, 1869)**

Giant Panda, Great Panda, Parti-colored Bear, Beishung, Bamboo Bear, White Bear, Panda Bear

Ursus melanoleucus David, 1869:13. Type locality vicinity of Mouping (Pao-hsing), Szechwan Province, China.

CONTEXT AND CONTENT. Content noted in generic summary above. The genus *Ailuropoda* is now monotypic.

DIAGNOSIS. The following diagnosis (from Davis, 1964 and Hendey, 1972) applies to both the genus and the species. Resembles other living bears in general body shape and proportions, but differs from them in distinctive coat color (figure 1), white with black eye patches, ears, fore and hind legs, stripe across shoulders, and sometimes tip of tail. Skull and mandible are robust (figure 2), sagittal crest is well developed, and zygomatic arches are expanded laterally and dorsoventrally relative to other arctoid carnivores (dogs, bears, raccoons and relatives). In contrast to characters of other living bears, the orbital fissure is confluent with the foramen rotundum, postorbital processes are reduced, alisphenoid canal is lacking; P4 is large, with prominent protocone and parastyle; M1 is roughly square, internal cingulum and multiple cusplets are present on M1 and M2; and M2 is elongated. An entepicondylar foramen is present, a primitive character shared, among living bears, only with *Tremarctos*.

GENERAL CHARACTERS. Head-body length is 1.2 to 1.5 m, tail approximately 127 mm, weight 75 to 160 kg. Coat is thick and woolly, color black (sometimes with brownish tinge) and white (sometimes reddish). Hind feet are not fully plantigrade—no heel pad; as in other bears the humerus is held firmly in place by a well-developed postscapular fossa. Dental formula is i 3/3, c1/1, p 4/4, m 2/3, total 42; first premolar is degenerate in both jaws and may be absent from the upper jaw; in contrast to those of other bears, second and third premolars are well developed; molars, particularly upper molars, are large relative to the skull, secondary cusps and tubercles (as in the European cave bear, *Ursus spelaeus*) are present on all molars. Muscles associated with mastication are large and both origins and insertions of jaw muscles are expanded. Vision is said to be poor and olfaction acute (Peking Zoo, 1974a). See especially Walker *et al.* (1964), Davis (1964), and Ewer (1973).

Davis (1964) provided an exhaustive and well-illustrated account of all aspects of the morphology of the giant panda. Goodwin *et al.* (1976) supplemented this monograph with studies of blood, alimentary tract, nervous system, eye, cranial arteries, vitamin D transport, mammary gland secretion, visual pigment (see also Dartnall, 1973), neurochemistry, cytochrome C, and transferrin. Cave (1974, 1975) published on the *sacculus epipharyngeus* and the thyroid and parathyroid glands in this species. Discussion of pathology and diseases of the giant panda can be found in several papers in Goodwin *et al.* (1976) and, also that of the Peking Zoo (1974b), which includes symptoms and

treatment of gastroenteritis, roundworm (*Ascaris* = *Baylisascaris schroederi*) (see also Sprent, 1968, and Giant Panda Expedition, 1974), respiratory tract infection, epilepsy, inflamed uterus, conjunctivitis, and inflamed bone marrow. Gastroenteritis and roundworm are the most common diseases of these animals.

DISTRIBUTION. Published data on the geographic range (figure 3) of the giant panda are equivocal and somewhat vague. The most recent reference to the range (Brambell, 1976) placed *Ailuropoda* in three main areas, possibly contiguous: southern Kansu (Min Shan), and northern and central Szechwan (Chiung-Hsia Shan = Chiung-lai Shan); southern Szechwan (Ta-liang Shan); and southern slopes of the Chin Ling (= Ch'in-ling), or Tapai Shan (= T'ai-pai Shan) of Sowerby (in Hsu, 1973), southern Shensi Province (the Chinese words shan and ling both refer to mountains). Older reports also place the giant panda in the Min Shan south of "Ssi-gu" (=Siku) on the Kansu-Szechwan border (Büchner and Berezovski, 1891), near Batang (= Pa-t'ang) (Edgar, 1972, 1930, in Hsu, 1973), "Yunwu Mountain" (not found—east of Pa-t'ang, Pen Hung-Shou, 1962), and at Oring Nor (= Cha-ling Hu), Tsinghai Province (Pen Hung-Shou, 1943). A recent unconfirmed report of four pandas found "in the hills to the north of Sining" (= Hsi-ning) (T'o-lai Shan, Tsinghai Province) also has appeared (Perry, 1969; Edgar, 1966, in Hsu, 1973). Morris and Morris (1966) suggested that the probable range extends from Tsinghai in the northwest to Shensi in the northeast and to Yunnan in the south. However, Wang Sung (Inst. Zool., Acad. Sinica, Peking—letter dated 14 April 1978) states that the occurrence of giant pandas in Tsinghai and Yunnan remains unconfirmed.

According to Wang Sung and Lu Chang-kun (1973), giant pandas range from 2700 to 3900 m above sea level; Brambell (1976) placed them between 2600 and 3500 m, the limits of the subalpine coniferous forest (Giant Panda Expedition, 1974) in which Chinacane bamboo (*Sinarundinaria*), the main food of the giant panda, grows in dense stands. Studies in the Wanglang Natural Reserve (Giant Panda Expedition, 1974) indicated that the distribution of these animals is limited below 2300 m but that they may occasionally descend to approximately 800 m in winter. Signs such as droppings and "claw prints" have been recorded as high as 4040 m.



FIGURE 1. Subadult *Ailuropoda melanoleuca* (courtesy National Zoological Park, Washington, D.C.).

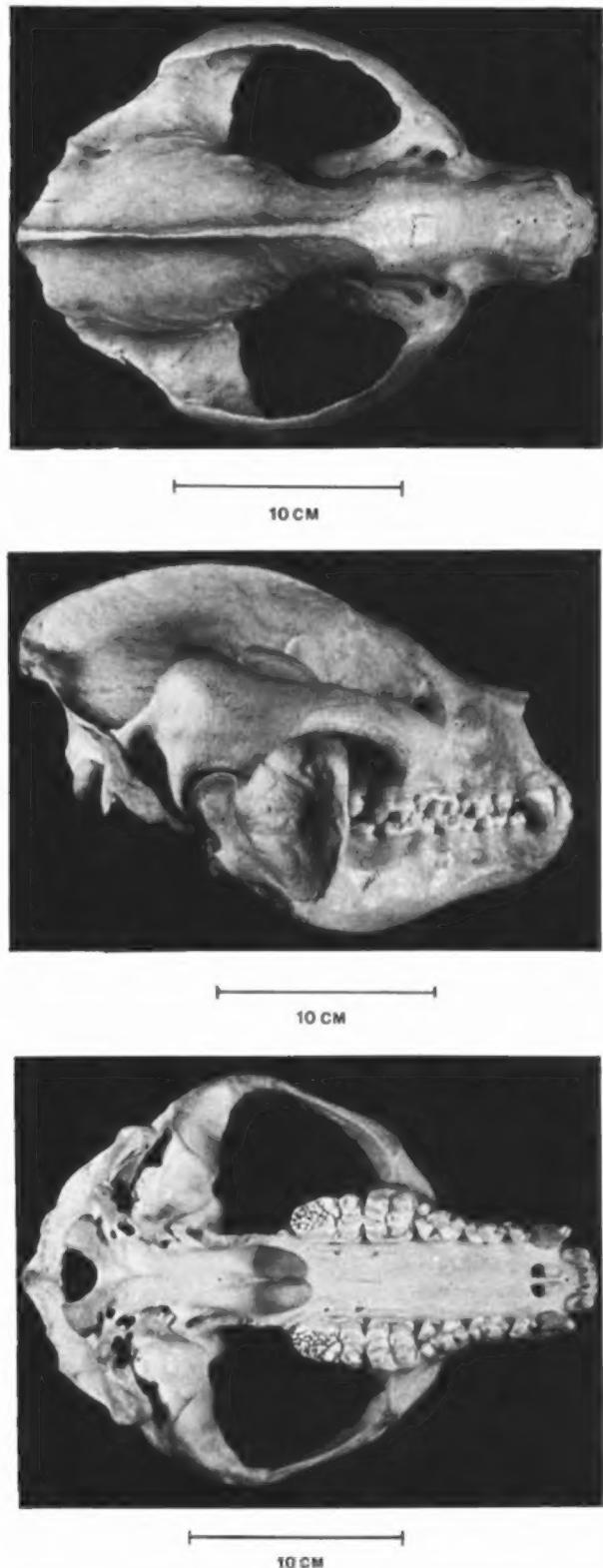


FIGURE 2. Skull (dorsal, lateral, and ventral views), and mandible (lateral) of adult female *Ailuropoda melanoleuca*, Cheng-wei, 7000 ft., 25 mi W Wenchwan, Szechwan, China, 17 November 1934 (AMNH 110451).

FOSSIL RECORD. According to Wang Sung and Lu Chang-kun (1973) the geographic range of the giant panda extended throughout southern China during the middle and late Pleistocene (see map, fig. 1, in Wang Tsiang-ke, 1974). Fossils are known from Szechwan, Yunnan, Shensi, Hupeh, Chekiang,

MAP
INSET
0 150 300 KM
0 150 200 MILES
WEST CENTRAL REGION
PEOPLES REPUBLIC OF CHINA

FIGURE 3. Present distribution of *Ailuropoda melanoleuca*. Stippled area, confirmed range (after Brambell, 1976); area enclosed by dashed line, potential range. Open circle, type locality; solid circles, specimen records (after Büchner and Berezovski, 1891; Davis, 1964; Hsu, 1973); question marks, unconfirmed sight records (Hsu, 1973; Pen, 1943, 1962).

Kiangsi, Fukien, Kwangsi, and Kwangtung provinces (figure 3). Middle Pleistocene material from Szechwan was described as *Aeluropus fovealis* (Matthew and Granger, 1923), and *Aelureidopuss baconi* was described (Woodward, 1915) from the Pleistocene of the northern Shan States in Burma. Davis (1964) placed both taxa in the genus *Ailuropoda*, and Wang Tsiang-ke (1974) further regarded the Burmese material as representing merely a large extinct subspecies, *Ailuropoda melanoluca baconi*, as did Colbert and Hooijer (1953) for *A. m. fovealis*. Pei Wen-chung (1962) described a small *Ailuropoda* from the early Pleistocene of Gigantopithecus Cave, Kwangsi, as *A. microta*. See Wang Tsiang-ke (1974) for tables of occurrences of fossil giant panda material and extensive specimen measurements.

The closest relatives of *Ailuropoda* (tribe *Ailuropodini*) are found in the extinct tribe *Agriotheriini*. Two genera of that tribe, the Pliocene *Indarctos* and the Plio-Pleistocene *Agriotherium* are allied with *Ailuropoda* within the subfamily *Agriotheriinae*. These three taxa are united largely on the basis of dental characters. All display a prominent protocone and a parastyle on the P4, and the M1 is roughly square and displays multiple cusplets (Hendey, 1972; see also Erdbrink, 1953). The subfamily includes a third tribe, *Tremarctini*, whose living representative is the South American spectacled bear, *Tremarctos ornatus*.

FORM. Davis (1964) revealed a close similarity between most of the organ systems in the giant panda and those of other bears. The histology of the bone does differ from that of *Ursus* due to greater thickness of the compacta in *Ailuropoda*. This is especially true in the skull and is correlated with the massive structure of the jaws and their use in chewing bamboo (Frayer *et al.*, 1978). Differences between giant panda and bear skulls, such as absence of the alisphenoid canal or of postorbital processes on the frontal bones, Davis ascribed to "expansion of the masticatory apparatus" (see also Chang *et al.*, 1960).

In the auditory bulla and subcranial region, and the carotid circulation in this area, *Ailuropoda* resembles *Ursus* in most respects, and differs markedly from typical procyonids (Segall,



FIGURE 4. Wild giant panda in typical sitting position in bamboo thicket, grasping stalk of bamboo on which it feeds (courtesy Wang Sung, Inst. Zool., Acad. Sinica, Peking).

1943; Davis, *op. cit.*; and especially Hunt, 1974). (*Ailurus*, the red panda, resembles ursids in basicranial but not in carotid anatomy.)

The manus of *Ailuropoda* is modified for grasping bamboo. This is achieved by an elongated radial sesamoid bone covered by a tough, fleshy, accessory lobe of the carpal pad and controlled by muscles that in other carnivores insert on the pollex (Wood-Jones, 1939). The radial sesamoid is opposable to the first two digits (Pocock, 1939) and is capable of a powerful grasp. The manus of *Ailurus fulgens*, the lesser or red panda, is also modified, with a fairly large radial sesamoid. However, *Ailurus* and all typical procyonids possess a *flexor brevis digitorum manus* muscle here, which is absent in *Ailuropoda* and other ursids (Davis, 1964; J. D. Lazell, Jr., personal communication).

Giant pandas differ from other living bears in that their alimentary system is highly specialized for the digestion of bamboo. The esophagus has a horny lining and the stomach is described as thick-walled and muscular, almost gizzardlike. The intestines are short, only five and a half times the overall body length. (The intestines of *Ailurus* also are relatively short.) The small intestine is most reduced, and perhaps little or no digestion takes place there. Surface area of the colon is enlarged relative to that of bears; there is no caecum in the giant panda. The liver is small and accessory lobes are reduced (Davis, 1964; Morris and Morris, 1966). (see also Chang and Lyu, 1959).

The urogenital system conforms for the most part with that of other arctoid carnivores, and the male accessory sex glands agree in structure with those of other bears. However, the external genitalia of the giant panda differ from those of all arctoids. Davis (1964) described the penis of *Ailuropoda* as being small, posteriorly directed, and subanal in position. The baculum is absolutely and relatively small; a short rodlike body with winglike expansions, unlike the baculum in any other carnivore. According to Davis (1964) the structure of the penis results from arrested development—"fetalization." Davis (*op. cit.*) also described the penis of *Ailurus* as "fetalized," but this is probably because Davis examined a young specimen (J. D. Lazell, Jr., personal com-

munication); the external genitalia of the adult male red panda is well developed, and does not resemble that in giant pandas, as Davis (1964) thought.

ONTOGENY AND REPRODUCTION. Estrus takes place in March, April, and May in the wild and in April and May in captivity (Peking Zoo, 1974a). The most intense heat occurs in late April and early May and it is then that mating occurs (Brambell, 1976). Duration of estrus is between four and 14 days but usually lasts approximately 10 days (Peking Zoo, 1974a). A second estrus may occur in autumn. Morris and Morris (1966—see also Walker *et al.*, 1964) speculated that fertilization or implantation may be delayed. Gestation takes approximately five months; for zoo-born giant pandas, gestation required 122 to 163 days (mean 140.2 ± 8 days—Peking Zoo, 1974a). The shortest period represents the birth of twins, one of which died, and may reflect premature birth. Time of birth is usually in September. Litter size normally is one or two; occasionally three young are born, but only a single young is ever raised by the mother (Brambell, 1976)—note, however, that Pen Hung-Shou (1943) reported sighting a female and two cubs in Tsinghai. Giant pandas are blind and toothless at birth, weigh between 90 and 131 g (104.2 g average) and are covered with sparse white fur (Peking Zoo, 1974a). According to Brambell (1976) the tail is long at birth, approximately one-third the body length, quite unlike that of other bears. Black fur begins to appear in the second week—first around the eyes, and soon thereafter on shoulders, limbs, and muzzle and paws in that order. Adult coloration is attained by the end of the first month. Eyes open between days 40 and 60 and coordinated vision is accomplished at approximately the third month. Independent feeding begins in the third and fourth months. By the sixth month young weigh approximately 13 kg and leave their mothers at this time. Studies by the Peking Zoo (1974a) reveal that the limbs of giant pandas are weak at birth and that it is two and a half months before the hind limbs can support the body. The young can walk and run by the middle of the fourth month. Teeth begin to erupt by approximately the third month. The report by the Peking Zoo (1974a) contains tables of body weight increase for the first year. Growth is rapid as in other bears. Sexual maturity varies but is usually attained in six or seven years (Peking Zoo, 1974a) (five or six years according to Brambell, 1976). Sheldon (1975) reported that giant pandas have lived 13 or 14 years in zoos but they probably live longer in the wild.

ECOLOGY AND BEHAVIOR. Climate of the region inhabited by the giant panda is generally damp. Summers are cool and the winters cold; rain, snow, and hail are common (Wang Sung and Lu Chang-kun, 1973; Morris and Morris, 1966). Temperature and humidity range from approximately -10°C and 90% r.h. (when air is above freezing) in winter, to 25°C and 60% in summer (Brambell, 1976). A partial list of the flora and fauna from the Wanglang Reserve, Szechwan, is in the report of the Giant Panda Expedition (1974). See also Roosevelt and Roosevelt (1929) and Sheldon (1975) for accounts of climate and habitat.

What giant pandas eat has been controversial since their discovery by Père David (Fox, 1949). Several authors have recounted statements by natives to the effect that giant pandas eat fish, pikas (*Ochotona*), and rodents. Brambell (1976) reported that their droppings sometimes contain the remains of bamboo rats (*Rhizomys pruinosus*). Bones have also been found in the stomach of a dead giant panda (Wang Sung and Lu Chang-kun, 1973; Giant Panda Expedition, 1974) so it seems that there is no longer any reason for believing that this animal is exclusively herbivorous or that it eats only bamboo. It has long been known that captive giant pandas will eat meat, and they are even said to steal meat from logging camps in the wild (Giant Panda Expedition, 1974). Bamboo (culms and leaves) is certainly the giant panda's chief food (McClure, 1943; Sheldon, 1975) but gentians, irises, crocuses, Chinese vines (*Lycium chinense*) and tufted grasses such as rice-grass and bent-grass are also eaten (Morris and Morris, 1966; Pen Hung-Shou, 1943). Fir bark is also eaten (Giant Panda Expedition, 1974) and reports of local natives indicate that these animals raid bee-hives for honey (Perry, 1969). Sheldon (1937) estimated that giant pandas may spend 10 to 12 hours a day feeding.

Giant pandas usually feed in a sitting position with the forelegs free to manipulate bamboo with the opposable radial sesamoid "thumb" (figure 4). In this position the animal grasps the bamboo stalk in its teeth and strips off the tough outer layer. The stalk is then fed into the side of the mouth, where a section at a time is thoroughly masticated. According to Davis (1964) the man-



FIGURE 5. Wild giant panda perched on branch of coniferous tree (courtesy Wang Sung, Inst. Zool., Acad. Sinica, Peking).

ual dexterity of the giant panda is good (see also Giant Panda Expedition, 1974; Collins and Page, 1973, for feeding behavior of *Ailuropoda*).

Knowledge of giant panda behavior is inadequate and awaits a detailed field study. They are known to bark and bleat. Wang Sung and Lu Chang-kun (1973) stated that their mating call is low and deep. Sound spectrograms of zoo animals were published by Morris and Morris (1966). Activity is mainly crepuscular, but captive giant pandas are also active at night (Kleiman, 1974) and this is probably true of wild giant pandas as well (Giant Panda Expedition, 1974). Captive females are known to mark "territory" with a scented, sticky secretion from the anal region (Morris and Morris, 1966). This is done with either a lateral or circular anogenital rub while in a squatting or quadrupedal stance. A female urinated "while lying flat on the venter with tail raised" (Kleiman and Collins, 1972). Males also mark with a lateral anogenital rub, and in addition they may use a "forward-back" rubbing movement after urinating with the leg cocked. Males also urinate against vertical surfaces while upright on forelimbs in a handstand (Kleiman and Collins, 1972; Kleiman, 1974; see also Collins and Page, 1969). In both males and females, urine and glandular secretions may be rubbed onto the back from a previously marked surface. Food, grass, ice, soil, and other materials often are rubbed onto the ventral surface with the forepaws (Kleiman and Collins, 1972).

Locomotion is similar to that of bears but with a longer stride. Unlike other bears, giant pandas do not gallop, but use a "diagonal walk," moving the limbs on one side forward and backward at the same time (Davis, 1964). They stand erect but never walk in this position. Posture is similar to that of other bears. "Play" behavior in young *Ailuropoda* is similar for males and females, and includes partial and complete somersaults, lateral rolls, and body twisting (Kleiman and Collins, 1972; see Wilson and Kleiman, 1974, for detailed account). Young giant pandas in the U.S. National Zoo are known to roll on their backs in the dirt while rubbing dirt over the throat and belly with their forepaws (Kleiman, 1975). These giant pandas also take water baths.

Opinion varies as to the climbing ability of the adult giant panda, and ranges from that of Sheldon (1975; see also Collins and Page, 1973) who believed that they seldom climb trees, to

that of Chinese workers (Giant Panda Expedition, 1974) and Brambell (1976) who described their climbing ability as excellent (figure 5; also see Giant Panda Expedition, 1974, for photographs of what is probably an adult giant panda descending a large fir tree). Although this response is by no means automatic (Sheldon, 1975), giant pandas sometimes climb trees to escape dogs (Walker et al., 1964; Morris and Morris, 1966; Giant Panda Expedition, 1974).

Other than females with young, giant pandas are solitary except during the breeding season when they may form groups of two or three (Giant Panda Expedition, 1974; Brambell, 1976).

Reports of native hunters indicate that the home range of a giant panda is small. It usually lives within a single ravine and remains within an area of 2.5 km, although during the rut it may move from one ravine to another (Giant Panda Expedition, 1974).

Chinese workers have estimated that approximately 200 giant pandas now inhabit the Wanglang Reserve and it is thought that this population is stable (Giant Panda Expedition, 1974). Brambell (1976) estimated that at least 1000 giant pandas survive in the wild, based on a conservative estimate of suitable habitat (6000 km²).

Giant pandas do not hibernate, but they do descend into lower ravines in winter and spring and are active on south-facing slopes. These animals make no permanent dens but take shelter in hollow trees, rock crevices, and caves (Giant Panda Expedition, 1974; Sheldon, 1975). Sheldon noted the occurrence of beds of bamboo, arranged in a circle beneath rock ledges and he suggested that such beds might be used as places to bring forth young.

Coat color may be aposematic (Morris and Morris, 1966), cryptic, or thermoregulatory (Lazell, 1974, 1976). Both Morris and Morris (1966) and Wang Sung and Lu Chang-kun (1973) discount the effectiveness of the dhole (*Cuon alpinus*) and leopard (*Panthera pardus*) as predators upon the giant panda. Probably only man poses a significant threat to this animal.

The first live *Ailuropoda* to be transported successfully out of China (Harkness, 1938) was exhibited during 1937-38 in the Chicago Zoological Park. Since then a number of giant pandas have been exhibited in Western and Chinese zoos (Morris and Morris, 1966; Perry, 1969), but breeding has occurred only in the latter. A detailed account of the management of captive giant pandas is given by the Peking Zoo (1974c). Claude (1971) summarized specimens known to have been collected through 1945.

GENETICS. The diploid (2n) number of chromosomes in *Ailuropoda* is 42; the karyotype includes 32 biarmed and eight acrocentric autosomes, one pair with prominent satellites (Newham and Davidson, 1966). Sex chromosomes were not positively identified, but in the female studied, the X chromosome was probably a medium-sized subtelocentric. Most bears, in contrast, have a 2n = 74 karyotype, with many (60 or more) acrocentrics. The exception is *Tremarctos ornatus*, the spectacled bear of the South American Andes, which has a 2n = 52, with only 20 acrocentric chromosomes, one pair of which bear prominent satellites as in *Ailuropoda* (Wurster, 1969). These satellites, or "marker," chromosomes resemble those seen in typical procyonids (2n = 38) and *Ailurus* (2n = 36), but are absent in other ursids.

REMARKS. One of the most interesting aspects of the giant panda is that for over a century it has seemingly defied classification. This is all the more strange considering that the anatomy of *Ailuropoda* is now well known. Only the domestic dog and cat have been more extensively studied anatomically among the carnivores. Summaries and references pertaining to the classification of the giant panda can be found in Davis (1964), Morris and Morris (1966), and Chu Ching (1974). Prior to the publication of Davis's (1964) anatomical study, British (Mivart, 1885; Lankester, 1901; Lydekker, 1901) and American (Gregory, 1936; Raven, 1936) workers generally supported the theory that *Ailuropoda* is most closely related to the supposed procyonid *Ailurus*. These two pandas were thought to be allied by extensive similarities of the dentition and skull structure, viscera, external genitalia, and the opposable sesamoid in the manus. Ewer (1973) also stressed the unbear-like behavior of *Ailuropoda*.

A second alternative is to separate the giant and lesser pandas from Recent bears and procyonids and place them in their own family(ies) (Ailuridae, Ailuropodidae—Pocock, 1921; Thenius and Hofer, 1960; Collins and Page, 1973). Todd and Pressman (1968) interpreted the karyotypes of the giant panda (2n = 42) and lesser panda (2n = 36) as possible support for this alternative.

Another alternative, a viewpoint held by most continental European workers, is that the giant panda is related to the bears. This was the position taken by Davis (1964) based on the general morphology of *Ailuropoda*. Serological studies, beginning with the work of Leone and Wiens (1956) on serum proteins, and Sarch's (1973, 1976) analysis of albumins and transferrins also indicate an affinity between *Ailuropoda* and Recent bears. Dental characters in particular ally the giant panda with two extinct bears, *Agriotherium* and *Indarctos* (Hendey, 1972; see also Bardenfleth, 1913). We believe that the weight of evidence now supports this relationship, and adopt it here. Most of the "specialized characteristics of giant pandas . . . also observed in lesser pandas but not in bears" (MacIntyre and Koopman, 1967), such as the manus and male genitalia, have now been shown to differ in *Ailuropoda* and *Ailurus*.

With few exceptions, panda systematics has suffered from the narrow scope of most taxonomic studies of the problem. The question of how closely *Ailurus* is related to other procyonids (or ursids) has also received too little attention. Assessment of shared derived characters, where these can be determined, based on available knowledge of anatomy, physiology, serology, karyology, behavior, and the fossil record of the pandas and other arctoid carnivores, is now necessary.

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